



THE GENUS *ARCHAEOCARIS*, AND A GENERAL
REVIEW OF THE PALAEOSTOMATOPODA
(HOPLOCARIDA: MALACOSTRACA)

FREDERICK R. SCHRAM

Natural History Museum, P.O. Box 1390, San Diego, California 92112 USA

Abstract. Newly discovered material of *Archaeocaris graffhami* Brooks, 1962, allows a more complete description and reconstruction of that animal. Reexamination of all specimens of *Archaeocaris* results in some modifications in the reconstruction of *Archaeocaris vermiformis* Meek, 1872, as well. All Paleozoic palaeostomatopod species are reviewed.

INTRODUCTION

Dr. Charles Sandburg of the United States Geological Survey in Denver, Colorado, referred some crustacean fossils to me for identification which proved to be *Archaeocaris graffhami* Brooks, 1962. The specimens were collected from the upper Pilot Shale at Bactrian Mountain in the Pahranaagat Range, Nevada, and effectively extend the stratigraphic range of this species from the Upper Mississippian, Chesteran, back into the Lower Mississippian, Kinderhookian.

This new material and my study of the British palaeostomatopods prompted a reexamination of all specimens of *Archaeocaris*. A general summary review of the entire order is presented, with a clarification of the relationships of *Archaeocaris* to the rest of the Palaeostomatopods.

SYSTEMATIC PALEONTOLOGY

Phylum Crustacea, Pennant, 1777
Class Malacostraca, Latreille, 1806
Subclass Hoplocarida, Calman, 1904
Order Palaeostomatopoda, Brooks, 1962
Family Perimecturidae, Peach, 1908
Genus *Archaeocaris*, Meek, 1872

Diagnosis.—Carapace smooth with posterodorsal margin deeply excavated to expose dorsum of posterior thoracomeres; mandible well sclerotized; uropods lobate; telson ovoid; body cross section circular to oval.

Archaeocaris graffhami Brooks 1962. (Figs. 1–3, 4b, 5a)

Brooks 1962, p. 214, Pls. 8 and 47; Schram 1969a, p. 217, Table 1.

Diagnosis.—Body moderate to large; weak development of mandible in relation to overall body size; abdominal pleura simple and undecorated; carapace thin and poorly sclerotized.

Remarks.—The holotype (part, Museum of Comparative Zoology at Harvard, 5849, and counterpart, University of Oklahoma, 4411) is poorly preserved (Fig. 5a).

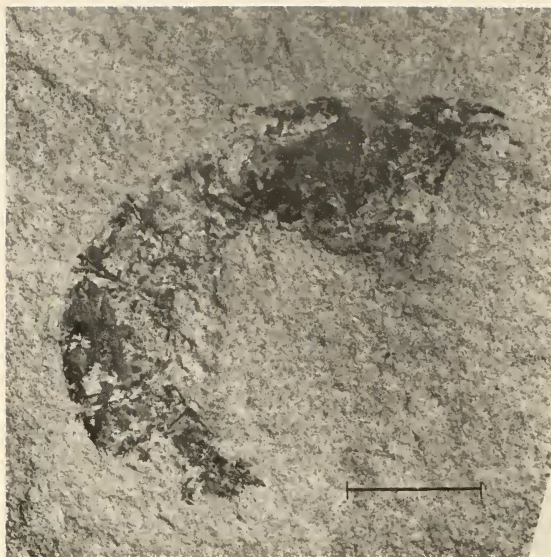


FIG. 1. *Archaeocaris graffhami* Brooks, 1962; USNM 220967; scale 1 cm.

Most of the tail is missing and there is no carapace. Indeed, as Brooks (1962) pointed out, only the ratio of the width of the mandible to body length, .023 (0.8 mm:35 mm) allowed these specimens to be distinguished from *Archaeocaris vermiformis*.

Additional material.—The new material from Bactrian Mountain consists of 3 specimens of more or less complete animals. USNM 220967 (Fig. 1), the largest and best preserved specimen, has a mandible width of 0.7 mm and an approximate body length of 41 mm, i.e., ratio of .017, somewhat smaller than for the types of *A. graffhami*. The body is generally poorly sclerotized, but the carapace is especially so, as seen on USNM 220967 and 220968 (Fig. 2). The tail fan, parts of which are seen on all 3 specimens, appears to consist of an ovoid telson and large lobate uropods, but again, unfortunately the preservation leaves something to be desired. USNM 220969 (Fig. 3) has pleopods preserved, and USNM 220967 and 220968 bear traces of cephalic and thoracic appendages, though little can be definitely determined for any of these except that the anterior thoracopods were subchelate. The deep excavation of the dorsal posterior margin of the carapace is evident on USNM 220967. Although the holotype counterparts are so poorly preserved that comparison with the Nevada specimens is difficult, the trapezoidal form and relative size of the mandible, the rounded shape of the abdominal pleurites, and the subchelate appendages seem to relate the entire group of specimens.

The associated fauna at Bactrian Mountain (Sandberg and Poole 1970) is an open marine, relatively deep water fauna of phosphatic brachiopods, *Chonetes*, sponge spicules, and ostracodes. Elias and Branson (1959) report a marine fauna in the Delaware Creek member of the Caney Shale in Oklahoma with the holotype of *A. graffhami*, including *Linoproductus*, the clam *Caneyella*, a snail *Macrocheilus*, several cephalopods, and abundant conodonts. Such a deep water, open marine association is unusual for Late Paleozoic malacostracans, which are more typically found in near-shoreline situations of shallow marine or brackish-freshwater habitats.

The range of *A. graffhami* is extended by inclusion of the material from Nevada. The lower and middle units of the Pilot Shale are dated on the basis of conodonts as

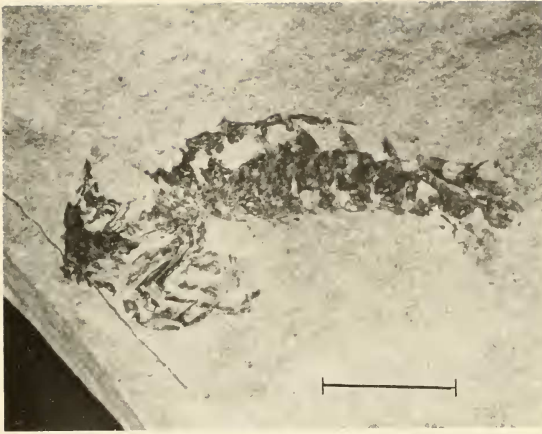


FIG. 2. *Archaeocaris graffhami* Brooks, 1962; USNM 220968; scale 1 cm.

latest Devonian; the upper Pilot Shale, which contains the shrimp, is lowermost Kinderhookian in age. The holotype comes from the Caney Shale, uppermost Meremecian or lowermost Chesteran in Pontotoc County, Oklahoma, USA.

Archaeocaris vermiformis Meek, 1872 (Figs. 4a, 5b, 5c)

Meek 1872, p. 335; 1875, p. 321, Pl. 18, Fig. 7; Ortmann 1897, p. 283; Van Straelen 1931, p. 71; Brooks 1962, p. 211, Pls. 8, 45, and 46; 1969, vol. R, p. R535, Fig. 341; Schram 1969a, p. 217, Table 1.

Diagnosis.—Body small; cuticle well sclerotized; relatively strong development of the mandible in relation to overall body size; abdominal pleura sculptured and marked with furrows.

Remarks.—The holotype and paratype series in the National Museum are not as well preserved as the series of specimens at Princeton University (Fig. 5b, 5c), 1597 d/1 to 1597 d/14. The treatment of Brooks (1962) remains substantially unchanged by me except for a few points resulting from preparation of the Princeton material.

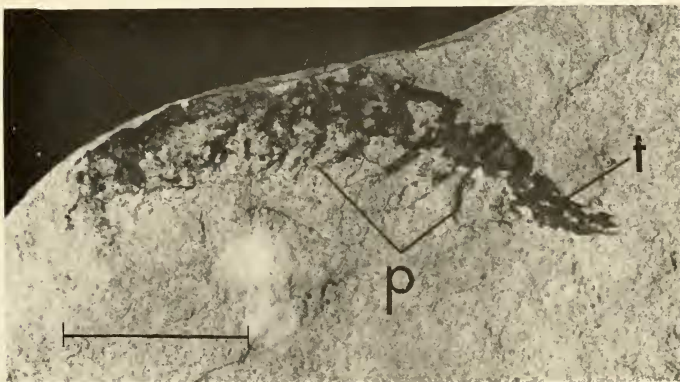


FIG. 3. *Archaeocaris graffhami* Brooks, 1962; USNM 220969; scale 1 cm. p = pleopods. t = telson.

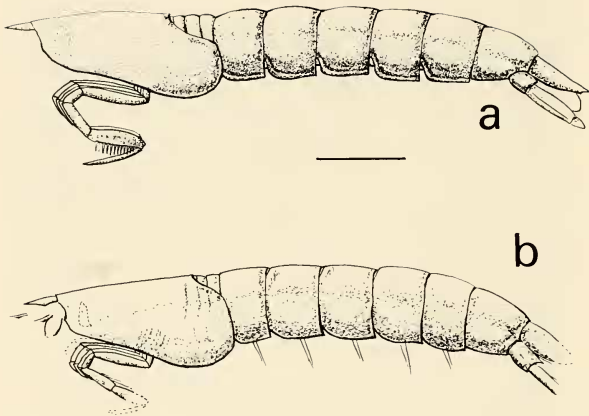


FIG. 4. Reconstructions of the species of *Archæocaris*, scale 1 cm. (a) *Archæocaris vermiformis* Meek, 1872. (b) *Archæocaris graffhami* Brooks, 1962.

Additional material.—The counterpart of 1597 d/1 to that illustrated in Brooks (1962, Pl. 46, Fig. 2) shows more clearly that the carapace extended along the midline to about the 6th thoracomere and the lateral wings of the carapace extended posteriorly to cover the pleurae of the last 3 thoracomeres, thus leaving the 3 posteriormost thoracomeres exposed dorsally. This arrangement of the carapace is also observable on 1597 d/7. In addition, 1597 d/1 also clearly preserved a series of large spines on the propodus segments of the anterior thoracic appendages opposed to the subchelate dactylus, thus forming a rather formidable battery of claws. 1597 d/2 and d/8 seem to indicate that the coxa of the anterior thoracomeres is short and that there is a moderately well developed precoxa proximal to the body. The telson and tail fan are still not well known. The uropods are visible as broad lobes on 1597 d/12, and to a lesser extent on d/4. The telson is smooth and undecorated, and has an oval shape, somewhat more pointed at the distal end (1597, d/4, d/12, d/13, d/14). There is no indication that the telson is developed terminally as a spike, as in *Perimecturus* and *Bairdops*, though there is some indication of terminally located, small caudal furca (1597 d/13).

Meek (1875) described *A. vermiformis* from the Waverly Group, near Danville, Kentucky in association with the phyllocarid, *Ceratiocaris*. The Waverly fauna is generally considered to be marine because the fauna contains such genera as *Fenestrella*, *Lingula*, *Orbiculoidea*, *Productus*, *Spirifer*, *Aviculopecten*, *Palaeoneilo*, *Schizodus*, *Platyceras*, and *Comularia*, among others. The Princeton material comes from west of Junction City, Boyle County, Kentucky, a site which also yielded a specimen attributed to *Palaeopalaemon newberryi*.

Genus: *Bairdops* Schram, 1979

Diagnosis.—Circular or oval in body cross section; carapace rectangular in lateral outline, no dorsally exposed posterior thoracomeres; telson base rectangular with prominent posterior spike. Uropods blade-like.

Remarks.—Two species of *Bairdops* are recognized: the Viséan *Bairdops elegans* (Peach) 1908 from the Calciferous Sandstone Series of Scotland, and the Namurian *Bairdops beargulchensis* Schram and Horner, 1978, from the Bear Gulch Limestone in the uppermost Mississippian of Montana, USA. The principal differences between the 2 species are these. The telson spike in *B. elegans* is more than half the length of the telson base. The uropodal protopod in *B. elegans* has only a slight middorsal

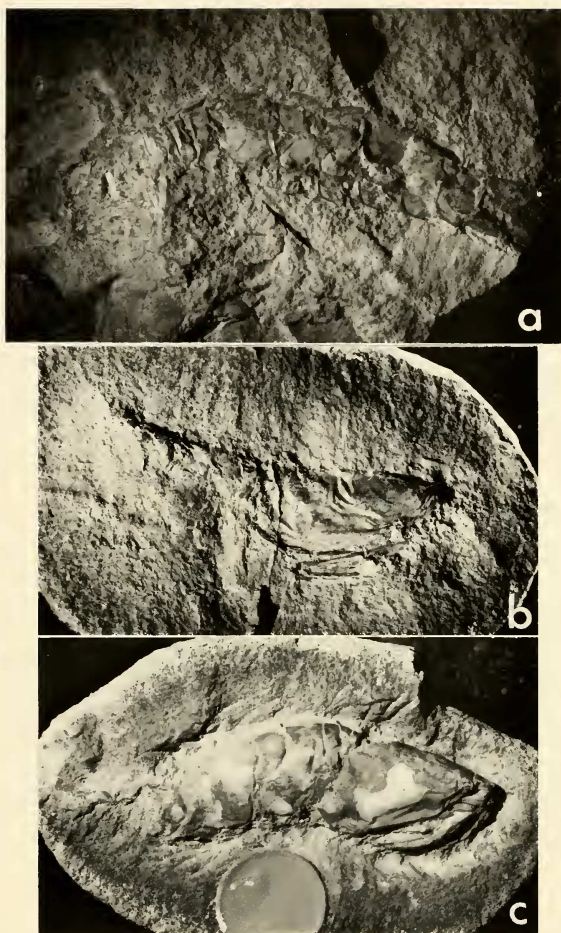


FIG. 5. (a) *Archaeocaris graffhami* Brooks, 1962; holotype MCZ 5849. (b) *Archaeocaris vermiformis* Meek, 1872; PU 1597 d/1 displaying the carapace and subchelate thoracopods. (c) *Archaeocaris vermiformis* Meek, 1872; PU 1597 d/3 displaying the abdominal pleurites.

posterior spike on the protopod. The uropodal exopod in *B. elegans* is a simple blade with no setae, while in *B. beargulchensis* it is laterally serrate and medially setose. The uropodal endopod of *B. elegans* is small and distally pointed with no setae, whereas in *B. beargulchensis* it is large, oval, and setose.

Although *Bairdops* is superficially similar to *Archaeocaris*, the former is generally larger. *Archaeocaris* has a carapace deeply excavated along the middorsal posterior margin, exposing several of the posterior thoracomeres dorsally, but *Bairdops* has no such excavation. In this regard, *Archaeocaris* is closer to the advanced tyrannophontid stomatopods, which reduce the length of the entire carapace and expose the 3 posterior thoracomeres completely. *Archaeocaris* does not have a telson spike and possesses thin, flap-like uropods, whereas *Bairdops* has a spiked telson and generally more blade-

like uropods. *Archaeocaris* again resembles the more advanced tyrannophontids, in regard to the unarmed telson whereas *Bairdops* is similar to *Perimecturus*.

Genus: *Perimecturus* Peach, 1882

Diagnosis.—Dorsoventrally flattened body. Telson base broadly triangular. Uropodal exopods strongly blade-like. Uropodal endopods small and atrophied.

Remarks.—There are 2 species of *Perimecturus*: the Viséan *Perimecturus parki* (Peach) 1882 in the Calciferous Sandstone Series of Scotland, and the Namurian *Perimecturus rapax* Schram and Horner, 1978, from the Bear Gulch Limestone at the top of the Mississippian of Montana. In addition, Brooks (1969) considered *Anthracomyia* Van Straelen, 1923, synonymous with *Perimecturus* but gave no reasons.

The differences between the 2 recognized species of *Perimecturus* are largely restricted to the tail fan. Long, delicate setae decorate the entire tail of *P. parki*, but *P. rapax* has no setae. The telson spike is less than half the length of the telson base in *P. rapax*. The uropodal protopod of *P. parki* is smooth and unadorned laterally, whereas that of *P. rapax* is distally serrate. The abdominal tergites and carapace of *P. parki* are decorated with 4 longitudinal ridges, but *P. rapax* has 3 ridges and scattered wart-like decorations.

The generally large size and distinct dorsoventral flattening of *Perimecturus* make it one of the most distinct of the Late Paleozoic malacostracans.

Order: Palaeostomatopoda *incerta sedis*

Rodendorf (1961, 1970) described supposed insect wings from the Upper Devonian of the USSR, *Eopterum devonicum* and *Eopteridium striatum*. Later he suggested (1972) these might be the uropods of palaeostomatopods. I have examined the original material in Moscow and agree, but am unable to give a definitive identification. They are definitely tail fans of some hoplocaridan or even eumalacostracan, but the specimens do not permit more precise identification.

Schram (1979) suggested *Perimecturus pattoni* Peach 1908 was not a palaeostomatopod, but possibly a tyrannophontid stomatopod.

Van Straelen (1923) described *Perimecturus fraiponti* from the Chokier Beds, Namurian, near Liege. From the description and illustration, however, the short carapace and completely exposed posterior thoracomeres would indicate this is a tyrannophontid stomatopod. The stratigraphic position of the material would tend to confirm this because palaeostomatopods are not found this high in the section.

DISCUSSION

Members of the subclass Hoplocarida were important constituents of Late Paleozoic crustacean faunas. Their morphological diversity and ecologic distribution exceeded that of modern hoplocaridans, now restricted to the highly specialized order, the Stomatopoda (mantis shrimp). The modern stomatopods are the only rapacious, active carnivores among the living crustaceans, other forms such as lobsters and crabs being scavenging, low-level carnivores. This rapacious trend in hoplocaridan evolution developed very early, by Early Mississippian or possibly Late Devonian time. The trend continued without interruption from the primitive palaeostomatopods through the Late Carboniferous archaeostomatopodan tyrannophontids into the Mesozoic, where essentially modern stomatopods are first encountered.

The Hoplocarida as a whole have fared poorly in comparison with the Eumalacostraca. Two of the 3 Paleozoic hoplocaridan orders, Aeschronectida Schram, 1969b, and the Palaeostomatopoda Brooks, 1962, became extinct in Permo-Triassic time, whereas the Paleozoic eumalacostracan superorders generally persisted to Mesozoic time and increased their morphologic diversity and geographic dispersion.

The singular success of the modern stomatopods is undoubtedly due to the evolution of complex behavior patterns used for a variety of purposes. Resources in limited

areas are partitioned with interspecific behavior patterns (Dingle et al., 1973), and complex patterns of behavior have evolved to communicate both within and between various stomatopod entities (Dingle 1969). In addition, the females of at least some species brood the young in cavities until stage IV molting occurs, effectively protecting the young until an advanced stage in development is reached (Dingle and Caldwell 1972), a habit found elsewhere only in the very successful peracarid eumalacostracans.

Caldwell and Dingle (1975) discuss the degree of armor and aggressive behavior in stomatopods. There are 2 types of raptorial appendages in living stomatopods, spearing and smashing forms. The smashers are the more vicious of the 2, possess heavy thoracic appendages with powerful muscles, display very intense and complex aggressive behavior patterns, have heavy telson armor, and tend to occupy rock or coral habitats. The spearers are not as heavily armored, less intense in their behavior, and burrow in soft substrates.

Such behavioral and morphologic parameters may have been at least incipiently at work in the palaeostomatopods. None of the palaeostomatopods can be considered heavily armored. The exoskeletons appear to have been only poorly to moderately sclerotized and no evidence of massive mineral deposits for armor is evident. In addition, the palaeostomatopods and tyrannophontid stomatopods had spearing type appendages. *Archaeocaris vermiformis* and *B. beargulchensis* clearly had serrate propodi on the thoracic raptorial subchelae. The habitats of all the palaeostomatopods seem to have been soft bottom and the dorsoventral flattened morphology of *Perimecturus* suggests a form adapted to lying partially buried and hidden in the sediment while waiting to ambush its next meal.

Modern stomatopod evolution seems to have moved from the less armored to the more armored, and there are indications the same might have occurred in paleostomatopod lines. For example, the tail fan of the Viséan *Perimecturus parki* is more delicately ornamented and seemingly not as well sclerotized than that of the simpler, blade-like, and serrated elements in the tail of the Namurian *P. rapax*. Viséan *Bairdops elegans* has a small undistinguished tail fan when compared to the spiked and serrate elements in the tail of *B. beargulchensis* of the Namurian.

As to what the events were that preceded the extinction of the palaeostomatopods and the rise of the stomatopods is difficult to assess. The success of stomatopods is undoubtedly related to the sophistication of their behavior. Palaeostomatopod behavior, aside from the generalities expressed above, is impossible to determine. Behavior in stomatopods is linked with limb specializations (Caldwell and Dingle 1975). Cisne (1974) used the Brillouin Expression ($h = [1/N] \log_2 [N! / (N_a! N_b! \dots N_s!)]$) to measure limb specialization and tagmatization, and employing this method the following values are obtained:

Palaeostomatopoda	2.12?
<i>Perimecturus parki</i>	
Archaeostomatopodia	2.25?
<i>Tyrannophontes theridion</i>	
Opisterostomatopodia	2.35
<i>Squilla mantis</i> .	

Some question exists for the exact values of the fossil groups. The morphology of the 1st thoracopod is unknown in any of these forms as to whether it is raptorial like the 2nd through 5th thoracopods (value of 2.12), or whether the 1st thoracopod is specialized in some way (value of 2.25) like that seen in the living stomatopods. It would seem from body morphology that the values given here express the lower level of palaeostomatopod limb specialization and body tagmatization, i.e., the stomatopod morphology (even that of the primitive tyrannophontids) was probably more effectively

able to handle the ecologic and behavioral parameters to survive as active, rapacious carnivores.

This replacement of palaeostomatopods by archaeostomatopodeans was going on by Namurian time in the middle of the Carboniferous. *Tyrannophontes* existed with palaeostomatopods in the uppermost Mississippian Bear Gulch Fauna (Schram and Horner 1978), and may have come into being somewhat earlier (Schram 1979). Later faunas such as the Middle Pennsylvanian, Westphalian C, Mazon Creek, Essex Fauna completely lack any palaeostomatopods (Schram 1969b, 1976).

KEY TO PALAEOSTOMATOPODA

Because the hoplocaridans and especially the palaeostomatopods are such important crustacean elements in Late Paleozoic faunas, a key is provided here to act as a guide in identifying the known forms.

- 1a. Seven segments in the abdomen Phyllocarida
- 1b. Six segments in the abdomen 2
- 2a. Abdomen and cephalothorax about equal in size Eumalacostraca
- 2b. Abdomen larger than cephalothorax 3
- 3a. Thoracic appendages unspecialized Aeschronectida
- 3b. Anterior thoracic appendages subchelate 4
- 4a. Carapace completely exposing the last 3 thoracic segments dorsally and laterally Tyrannophontidae
- 4b. Carapace covering all thoracic segments, at least laterally 5
- 5a. Carapace covering thoracic segments dorsally and laterally, telson with prominent, terminal spike 6
- 5b. Carapace excavated along dorsal, posterior margin to expose dorsal portion of thoracomeres, telson suboval with no prominent spike 9
- 6a. Body dorsoventrally flattened (*Perimecturus*) 7
- 6b. Body subcylindrical (*Bairdops*) 8
- 7a. Telson spike less than half the length of telson base, entire tail fan with long, hair-like setae, uropodal protopod with posterior spike between endo- and exopods *Perimecturus parki*
- 7b. Telson spike more than half the length of telson base, no setae, endopods distally serrate, and telson serrate near caudal furca, uropodal protopod with posterior spike flanking the telson *Perimecturus rapax*
- 8a. Tail fan without setae or serrations, telson spike less than half the length of telson base *Bairdops elegans*
- 8b. Uropod margins setose, uropodal exopod laterally serrate, telson spike more than half the length of the telson base *Bairdops beargulchensis*
- 9a. Exoskeleton moderately well sclerotized, abdominal pleura sculptured and marked with furrow, mandible well developed with a mandible width: body length ratio approximately .043 *Archaeocaris vermiformis*
- 9b. Exoskeleton thin and poorly sclerotized, abdominal pleura simple, mandible-width:body ratio about .023 or less *Archaeocaris graffhami*

LITERATURE CITED

- Brooks, H. K. 1962. Paleozoic Eumalacostraca of North America. *Bulletins of American Paleontology* 44(202):163-338.
- . 1969. Palaeostomatopoda. Pages R533-R535 in R. C. Moore, editor. *Treatise on Invertebrate Paleontology*, Part R, Arthropoda 4(2). Geological Society of America and University of Kansas Press.
- Caldwell, R. L., and H. Dingle. 1975. Ecology and evolution of agonistic behavior in Stomatopods. *Die Naturwissenschaften* 62:214-222.
- Cisne, J. L. 1974. Evolution of the world fauna of aquatic free living arthropods. *Evolution* 28:337-366.
- Dingle, H. 1969. A statistical and informational analysis of aggressive communication in the mantis shrimp *Gonodactylus bredini* Manning. *Animal Behaviour* 17:561-575.
- , and R. L. Caldwell. 1972. Reproductive and maternal behavior of the mantis shrimp *Gonodactylus bredini* Manning. *Biological Bulletin* 142:417-426.

- Dingle, H., R. C. Highsmith, K. E. Evans, and R. L. Caldwell. 1973. Interspecific behavior in tropical reef stomatopods and its possible ecological significance. *Oecologia* 13:55-64.
- Elias, M. K., and C. C. Branson. 1959. Type section of the Caney Shale. Oklahoma Geological Survey, Circular 52. 24 pp.
- Meek, F. B. 1872. Descriptions of new western Paleozoic fossils, mainly from the Cincinnati group of the Lower Silurian Series of Ohio. *Proceedings of the Academy of Natural Sciences of Philadelphia* 24:335-336.
- . 1875. Invertebrate fossils of the Waverly Group and Coal Measures of Ohio. Report of the Geological Survey of Ohio 2(2):273-325.
- Ortmann, A. E. 1897. The systematic position of *Crangopsis verniformis* (Meek) from the subcarboniferous rocks of Kentucky. *American Journal of Science, Series 4*, 4:283-289.
- Peach, B. N. 1882. On some new Crustacea from the Lower Carboniferous rocks of Eskdale and Liddesdale. *Proceedings of the Royal Society of Edinburgh* 30:73-91.
- . 1908. A monograph on the higher Crustacea of the Carboniferous rocks of Scotland. Geological Survey of Great Britain, Paleontological Memoirs 1908. 82 pp.
- Rodendorf, B. B. 1961. Opisanie pervogo krilatogo nasekomogo iz devonskikh otlezhenii timana (Insecta, Pterygota). *Entomologicheskoe obozrenie* 40:485-489.
- . 1970. Vtoraya nadhodka ostatkov krylatykh Devonskikh nasekomykh. *Entomologicheskoe obozrenie* 49(4):835-837.
- . 1972. Devonskie zotsteridy—ne nasekomye, a rakoobraznie Eumalacostraca. *Entomologicheskoe obozrenie* 51(1):96-97.
- Sandberg, C. A., and F. G. Poole. 1970. Conodont biostratigraphy and age of West Range Limestone and Pilot Shale at Bactrian Mountain, Pahrnagat Range, Nevada. *Geological Society of America Abstracts with Programs* 2(2):139.
- Schram, F. R. 1969a. The stratigraphic distribution of the Paleozoic Eumalacostraca. *Fieldiana: Geology* 12:213-234.
- . 1969b. Some Middle Pennsylvanian Hoplocarida and their phylogenetic significance. *Fieldiana: Geology* 12:235-289.
- . 1976. Some notes on Pennsylvanian crustaceans in the Illinois Basin. *Fieldiana: Geology* 35:21-28.
- . 1979. British Carboniferous Malacostraca. *Fieldiana: Geology* 40:1-129.
- , and J. Horner. 1978. Crustacea of the Bear Gulch Limestone, Mississippian of Montana. *Journal of Paleontology* 52:394-406.
- Van Straelen, V. 1923. Quelques Eumalacostracés nouveaux du Westphalien inférieur d'Argenteau près Liège. *Annals de la Société Géologique Belgique* 45:m35-m40.
- . 1931. Crustacea Eumalacostraca. *Fossilium Catalogus, Animalia Part* 48. 98 pp.